HOW SEA STARS OPEN BIVALVES[1]

MARCEL E. LAVOIE[2]

Syracuse University, Syracuse, N. Y.

The damage inflicted upon the oyster and clam industries by sea star predation (Galtsoff and Loosanoff, 1939; Barnes, 1946) has stimulated much interest in the method employed by asteroids to open the shells of bivalve molluscs. The many solutions proffered in the past were reduced to two probable alternatives within the last sixty years: (1) the "toxin" theory which proposes that sea stars secrete a substance which produces relaxation of the adductor muscles of their victims; and (2) the "mechanical" theory which credits the sea stars with the ability to pull the valves of the molluscan shell apart by means of their tube feet.

The first hypothesis was proposed originally by Eudes-Deslongchamps (1826). Most of its advocates (including Hesz, 1878; Figuier, 1891; Pieron, 1913; Cahn, 1950; Korringa, 1953 and Aldrich, 1954) postulated that the chemical agent was secreted by the digestive organs of the sea stars. Van der Heyde (1922) and Sawano and Mitsugi (1932) supported this view with experiments which demonstrated that extracts of asteroid stomach and/or pyloric caeca produce tetanus and, often, permanent cessation of cardiac beat when poured over the hearts of living molluscs.

The mechanical theory, advanced originally by Fischer (1864) and Bell (1892), was established firmly by Schiemenz (1895) who demonstrated experimentally that the valves of the clam *Venus verrucosa* could be separated by a pull of 900 grams, while a clam held by the tube feet of an *Asterias* could be released only if a pull of more than 1000 grams was applied to it. He concluded that the sea star could exert a pull greater than that which could be sustained by *Venus*, but he failed to note that he had measured only the adhesive capacity of the echinoderm's tube feet. He did not show that the sea star possessed the ability to produce sufficient muscular force to open bivalves. However, it is believed that the data presented below demonstrate the existence of such forces and render the toxin theory less tenable.

MATERIALS AND METHODS

The two groups of experimental procedures employed were designed to determine (1) the effects of sea star extracts upon a representative bivalve, and (2) whether sea stars actually pull upon the valves of their prey.

1. *Procedures for determining effects of extracts*

The stomach and/or pyloric caeca of *Asterias forbesi* (obtained from the Marine Biological Laboratory at Woods Hole) were excised and ground with a Pyrex glass

---

[1] This investigation is a portion of a dissertation submitted in partial fulfillment of the requirements for the degree of Doctor of Philosophy in the Department of Zoology at Syracuse University in September, 1955.

[2] Present address: Department of Zoology, University of New Hampshire, Durham, New Hampshire.

homogenizer in the cold. Enough sea water or distilled water was added to make up 10% solutions relative to the wet weight of the organs used. (Other concentrations were tested and, generally, yielded similar results.) Extraction was allowed to proceed for varying times (5 minutes to 48 hours) and the tissue debris was removed by filtration or centrifugation. Other extraction methods were employed to test the possibilities that the alleged toxin might be only poorly soluble in water, that it might occur in bound form, or that it might require activation. Thus, some extractions were made with fat solvents, some extracts were dialyzed, others were frozen and thawed before use, and some were mixtures of homogenates from different organs.

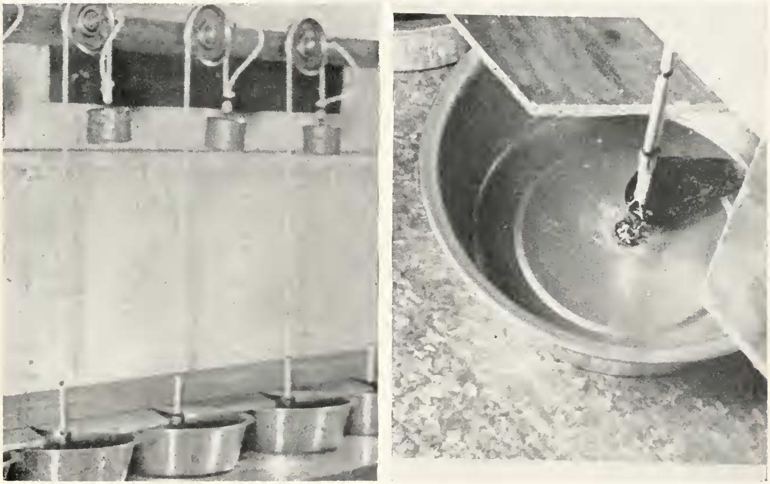
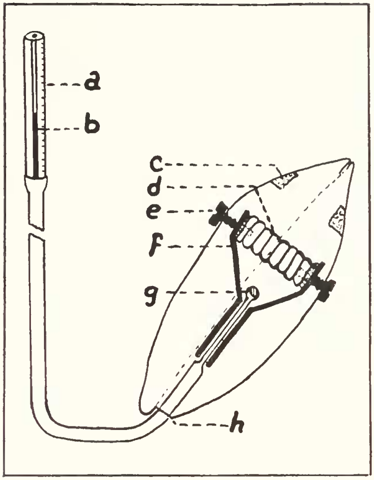


FIGURE 1. Constant stress apparatus. Each 800-gram weight was suspended by a cord passing over a ball-bearinged pulley to a double hook inserted into notches filed in the beak of the mussel shell. Another hook, also made from two bent pins, was soldered to the bottom of the pan and passed through the same notches. Gapes were measured by means of a calibrated metal triangle which could be slipped in between the valves near the hooks.

All extracts were tested on the common sea mussel, *Mytilus edulis*. In most cases 0.5 ml. of the clear extract was injected by means of hypodermic syringe into the mantle cavity or 0.15 ml. was injected directly into the posterior adductor muscle by way of a notch filed in the shell's dorsal edge. Each mussel had been pre-tested to insure that its physiological condition was approximately comparable to that of the other experimental animals. The pre-test was accomplished by exerting a pull of 800 grams on the valves for five minutes; only mussels which gaped less than one mm. were used for injection tests. After being injected, each mussel was subjected to a steady pull of 800 grams on its valves (Fig. 1) for 45 minutes during which measurements of the gape were made at regular intervals.

In some cases, the extract was merely added to the sea water into which the mussel was placed after having been kept out of water for 12 hours, and the gape was determined after 5 and 10 minutes. In other experiments, the mussel heart was exposed and perfused with the extracts while kymograph records were made of the effects on the beat. Controls for all types of tests were treated with solvent only (sea water or distilled water) or with extracts of other sea star organs or extracts of the digestive organs of other invertebrates.



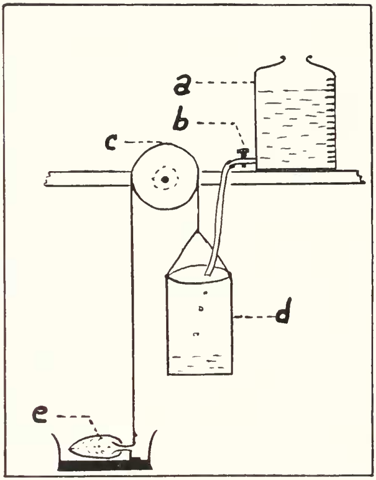


FIGURE 2. Apparatus for measuring sea star pulling force. The device and the mussel are represented at approximately actual size. *a.* calibrated capillary tube; *b.* water column; *c.* cut posterior adductor muscle; *d.* steel coil spring; *e.* bolt; *f.* metal plate soldered to the spring; *g.* plugged end of water-filled rubber tube; *h.* cut umbo. In some experiments this manometric unit was replaced by a plastic cylinder which fitted between the two bolts.

FIGURE 3. Increasing load stress apparatus. *a.* calibrated water jar; *b.* control valve; *c.* pulley; *d.* waxed cardboard container; *e.* mussel. The approximate total load applied to the shell was computed by adding the container weight to the weight of the water poured into it from the calibrated jar.

2. *Procedures for determining sea star pulling ability*

The adductor muscle of medium-sized *Mytilus* was severed with a thin razor blade and the valves were then made to shut firmly by means of an "artificial muscle." This consisted of a tightly coiled steel spring about ½ inch long with a metal plate soldered at each end. The spring was held in place (Fig. 2) by short bolts inserted through holes bored in the valves. The metal plates were bent so as to compress the sealed end of a water-filled rubber tube which passed out of the shell through a hole effected by breaking off one tip of the umbo. The distal end of the rubber tube was slipped over the end of a graduated capillary tube. Any outward pull on the valves was reflected in the stretching of the spring and, consequently, in an increased volume of the rubber tubing and a lowering of the water level in the manometer tube. The variations in water level, produced by a sea star humped over a mussel containing this apparatus, could be duplicated by inserting the mussel, afterward, in the stress apparatus illustrated in Figure 3. In some instances, the severed adductor muscle was replaced by a threaded plastic cylinder so that the valves could be bolted together firmly or allowed to separate only slightly.

Table I

Gaping of Mytilus under stress. These raw data are from two representative groups of experiments involving the application of stress to the shells after injections into the adductor muscles. The apparatus permitted the testing of 10 mussels simultaneously; generally, five were treated with extract and five with control solutions. Shells ranged in size from 43 × 22 mm. to 55 × 30 mm.

Injected with	Gape in millimeters after					
	5 min.	10 min.	15 min.	20 min.	25 min.	45 min.
Distilled water	0	0	0	0	0	0
	0	0	0.7	2.0	0.2	2.0
	0	0	4.8	4.0	5.8	7.8
	0.5	0	9.6	0.2	2.8	2.2
	0.9	2.8	1.7	1.8	2.8	1.8
	2.2	2.5	2.7	2.7	2.5	2.5
	2.8	2.9	3.8	3.0	3.8	3.2
	3.5	3.2	3.2	3.8	3.5	4.0
	3.8	4.8	4.9	5.0	5.0	5.5
	3.8	4.0	3.8	4.8	5.7	6.2
Pyloric caeca in distilled water	0	0	0	0	0	2.2
	0	0	0	0	0	4.8
	0	0	0	0.8	3.7	4.8
	1.8	1.8	1.9	3.0	3.0	2.8
	1.7	3.0	3.2	3.0	3.0	2.0
	1.8	1.8	1.8	1.8	1.9	5.8
	2.1	2.1	2.1	2.2	2.5	3.0
	3.8	3.8	3.8	5.0	5.3	5.4
	4.0	4.0	3.8	4.0	4.8	4.8
	4.8	5.7	5.8	5.8	5.8	4.8

Results

1. *Effects of sea star extracts*

As reported by previous investigators, extracts of the digestive organs of sea stars generally produce tetanus in molluscan hearts. But so do other substances including sea water. Furthermore, any suggestion that an asteroid secretion may affect the adductor muscle indirectly by stopping the heart seems untenable in view of the observation, made in some of these experiments, that *Mytilus* whose hearts are excised may continue to maintain their valves tightly shut for two or three days.

Mytilus placed in sea water contaminated with sea star extracts usually "taste" the medium and then close their valves firmly. The degree of gaping, among the sixty mussels tested in this manner, was less for specimens exposed to diluted extracts than for those placed in sea water alone. This seems to indicate that no muscle-relaxing toxin was present in the extracts.

Gape measurements made on mussels injected with extracts or control solutions revealed that the rate of shell opening varied through a very narrow range for all tests. The average value of the rate of gaping for mussels which were not injected was almost identical to that of mussels whose mantle cavity or adductor had been injected with sea water or distilled water or with one of the various types of extracts (see representative data in Table I). Over 1000 mussels were tested in this manner and the data can only lead to the conclusion that the extracts did not contain any substance which could be considered effective in inducing relaxation of the bivalve adductor muscles.

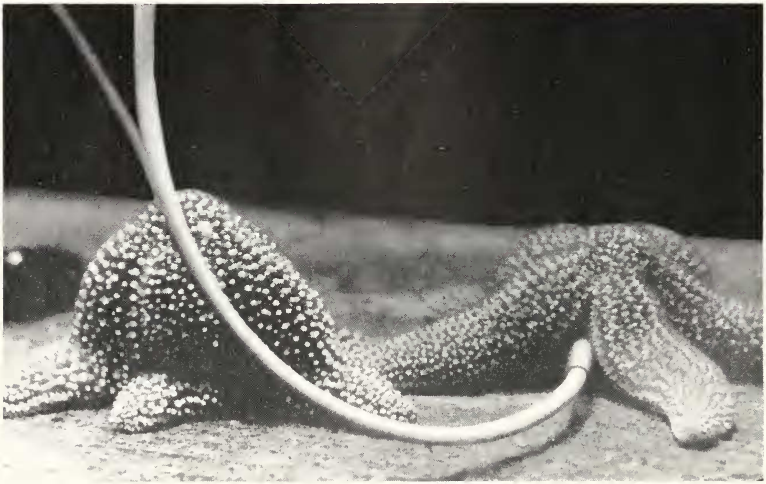


FIGURE 4. *Asterias* feeding upon decoy mussels. The rubber tube leading to the manometric recorder is covered with a glass sleeve near the mussel in order to prevent compression of the tube by the sea star's antimeres. The asteroid on the left is in the process of inserting its stomach into a shell whose valves are tightly bolted together by means of plastic cylinder.

2. *Observation of sea star pulling ability*

Sea stars, kept in 20-gallon tanks of circulating sea water, were presented live mussels whose adductors had been replaced by springs or cylinders as described previously. The soft parts of most of these mussels were reached by the asteroid stomachs and were partly or wholly digested. Unquestionably, no secretion of the sea stars could have had any weakening effect upon the "artificial muscles" holding the pelecypod valves closed. The following cases, selected from several dozen observations, illustrate the significance of the results obtained:

1) A sea star was observed while it approached a mussel containing the spring device and while it humped over its victim in the typical predatory position (Fig. 4). During the five minutes it required to settle in an advantageous position (and, probably, to extrude its stomach) there was no change in the water level of the recording apparatus. During the next three minutes, however, the level dropped rapidly; at the end of this time the sea star was removed from the aquarium and its arms were peeled back forcibly in order to expose the mussel. The valves were found closed tightly upon the sea star's stomach, most of which was inserted into the shell. In this case, the drop in the recording tube was duplicated later with a load of 1200 grams on the shell's valves; but spring-containing mussels requiring 2600 to 3000 grams pull to open 0.1 mm. were also successfully preyed upon by the sea stars.

TABLE II

Summary of pulling forces exerted by a sea star upon a spring-containing mussel

Time (in minutes) from beginning of observation	Pulling force (in grams) applied by the sea star
0	440
5	740
10	620
14	710
15	560
20	620
60	470
90	0
115	650
135	0
150	680
155	800
158	0
159–165	Sea star moved off mussel

2) Another *Asterias* was observed for almost three hours after it was found humped over a prepared mussel. During that time, the water level of the recording tube varied through three irregular cycles of rises and falls. When these variations were duplicated later by placing the mussel in the stress apparatus, it was seen that they represented the pulling forces shown in Table II. When the mussel was opened it was found to be partly digested. This, and many similar observations, seems to indicate that the sea star's pull is not applied steadily.

3) A mussel whose valves were bolted together very firmly so that no space could be discerned between them under 9 × magnification, was loosened forcibly from the grasp of a sea star that had humped over it for several hours. The asteroid's stomach was mostly inside the shell and it did not slip out again during the next hour while the sea star dragged the shell along the bottom of the aquarium. Later, when the shell was exposed to increasing loads in the stress apparatus, the valves were bent enough by a load of 3100 grams to produce an opening between them of 0.1 mm.

4) Several mussels whose valves were tied together so as to open only 0.1 mm. were invaded by sea stars whose stomachs were seen to slip out of the shells when the echinoderms' arms were pulled away from the shells.

DISCUSSION

The negative results of the experiments involving sea star extracts are not proof that asteroids do not secrete a toxin during predation, but they do indicate that no such substance can be separated from the sea star organs by the extraction methods used. Furthermore, a muscle-relaxing secretion would seem superfluous, at least in the predation of *Asterias forbesi* upon *Mytilus edulis,* since it was shown above that this asteroid is capable of producing a pulling force which is transmitted to the valves of mussels by the anchoring action of the tube feet.

It may be questioned whether some species of pelecypods which are attacked by sea stars might not require stronger pulls to open than those that can be mustered by *Asterias.* Reese (1942) showed that 3750 grams could be withstood for several days by some *Venus* and *Ostrea;* Tamura (1929) reported that the Japanese oyster may sustain 15,000 grams pull for as long as five minutes; Galtsoff (1952) referred to the ability of oysters to withstand 6000 grams for several hours; Plateau (1884) computed *Ostrea's* "absolute resistance" (equal to the force required to open its shell one mm.) at 5026 grams, while Marceau (1909) reported that *Mytilus* could withstand a pull of 11.3 kg./sq. cm. of its adductor muscle tissue.

These impressive figures seem to preclude any possibility that sea stars pull open the shells of *Ostrea* and *Venus.* But, on closer examination, Plateau's "absolute resistance" appears outstandingly significant—if a force of 5026 grams can produce an opening of one mm. in *Ostrea,* might not a lesser pull be sufficient to open the shell 0.1 mm., the smallest measured gape through which sea stars' stomachs have been observed to penetrate? Many of the objections to the mechanical theory in the past have been based on the supposition that much larger gapes would be required (Reese proposed 7 mm. as a minimum), and the fact that such wide openings could be effected only by tremendously strong forces which a sea star could not be expected to exert. The experimental results described above have shown that *Asterias* is capable of producing pulling forces equivalent to 3100 grams. It seems likely that even greater forces could be demonstrated with adequate apparatus. Therefore, there is little reason to suppose that the usual bivalve prey of sea stars cannot be opened by the attached tube feet, at least enough for the insinuation of the stomach. According to this view, only very large and highly resistant molluscs would be immune to sea star predation. In fact, the larger, more resistant *Mytilus edulis* are seldom attacked successfully by sea stars. However, Feder (1955) reports that the larger *Mytilus californianus* are eaten by asteroids, but that entry into the shell is gained by way of the mussel's byssus "door" which is relatively wide in that species. By contrast, only one among the hundreds of east coast *Asterias* observed during this research was seen to have employed this approach. Feder also measured forces and shell openings which closely approximate the figures reported herein.

It must be emphasized that the observations made during this investigation do not support the popularly accepted notion that the process of predation is a "tug-of-war" in which the sea star becomes the victor by virtue of its persistence and greater endurance. The penetration is effected, as shown above, quite rapidly and as the result of a sudden overwhelming force, which is relaxed and re-applied at intervals until digestion of the soft parts of the bivalve has proceeded to the point where the adductor muscle is rendered ineffective.

The exact mechanism responsible for the pulling force has not been established. However, it is thought to reside in the musculature of the tube feet described in detail by Smith (1937, 1947). Once humped over the bivalve, the asteroid's body moves very little or not at all, but the tube feet are very active, protracting and retracting in such a way that they give the impression of operating in relays. Each tube foot's muscular tissue is ample to overcome the 29 grams of adhesiveness of the base (Paine, 1926). If this value is used as a criterion, then, it would appear that a sea star would need to employ less than one-fourth of all its tube feet simultaneously to produce pulls of over 5000 grams.

SUMMARY

1. An investigation was made into the possibility that sea stars secrete a substance which is toxic or anesthetic for bivalves. Extracts prepared from the organs of feeding and non-feeding *Asterias forbesi* were introduced into the adductor muscle and the mantle cavity, or perfused over the beating heart, of *Mytilus edulis.* The effects of such solutions were, generally, identical to those produced by sea water or distilled water.

2. Sea stars were induced to feed upon specially prepared mussels, so that the forces which their tube feet exerted on the shells could be measured manometrically. The adductors of the mussels used in such experiments had been severed and replaced by steel springs or plastic cylinders which could not be affected by any alleged toxin. It was found that the tube feet did pull the valves apart and forces of over 3000 grams were recorded. It was observed also that a very minute opening between the valves (0.1 mm.) was sufficient to permit the insinuation of the asteroid stomach.

3. The common interpretation of the mechanical theory, which asserts that the sea star "fatigues" the mollusc, appears inaccurate in view of the findings of this research. There is evidence that the opening of the valves is a rapid process involving overwhelming, discontinuous forces, so that the predator may be considered to relax its pull upon the valves at intervals and to allow its stomach to be compressed between the valves until it pulls them apart again.

LITERATURE CITED

ALDRICH, F. A., 1954. On the functional morphology of the alimentary canal of the sea star *Asterias forbesi* Desor. Ph.D. thesis, Rutgers University.

ALLEN, E. J., 1896. How do starfishes open oysters? *J. Mar. Biol. Assoc.,* **4**: 266–285. (English translation of a paper by Schiemenz, 1895.)

BARNES, E. W., 1946. Starfish menace in Southern Mass. in 1931. *Bull. Bingham Ocean. Coll.,* **9**: 38–43.

BELL, F. J., 1892. Catalogue of the British echinoderms in the British Museum. Longmans and Co., London.

CAHN, A. R., 1950. Oyster culture in Japan. *Fisheries Leaflet,* **383**: 1–80. Washington.

EUDES-DESLONGCHAMPS, H., 1826. Notes sur l'Astérie commune. *Ann. Sci. Nat. Paris (Zoologie),* **9**: 219–221.

FEDER, H. M., 1955. On the methods used by the starfish *Pisaster ochraceus* in opening three types of bivalve molluscs. *Ecology,* **36**: 764–767.

FIGUIER, L., 1891. The ocean world. Cassell and Co., London.

FISCHER, P., 1864. Faune conchiologique marine du Department de la Gironde. *Act. Soc. Linn. Bordeaux,* **25**: 257–344.

GALTSOFF, P. S., 1952. How strong is the oyster? Addresses delivered to the National Shell Fisheries Association, pp. 51–53.

GALTSOFF, P. S., AND V. L. LOOSANOFF, 1939. Natural history and control of the starfish. *U. S. Bur. Fish. Bull.,* **31**: 75–132.

HESZ, W., 1878. Die werbellosen Tiere des Meeres. Hanover.

VAN DER HEYDE, H. C., 1922. On the physiology of digestion, respiration, and excretion in echinoderms. C. de Boer Jr., Amsterdam.

KORRINGA, P., 1953. Oysters. *Sci. Amer.,* **189**: 86–91.

MARCEAU, F., 1909. Contraction of molluscan muscle. *Arch. Zool. Exp. Gen.,* **2**: 295–469.

PAINE, V. L., 1926. Adhesion of the tube feet in starfishes. *J. Exp. Zool.,* **45**: 361–366.

PIERON, H., 1913. Sur la manière dont les poulpes viennent a boût de leur proie, des lamellibranches en particulier. *Arch. de Zool. Exp. Gen.,* **53**: 1–13.

PLATEAU, F., 1884. Force absolue des muscles des invertèbres. *Arch. de Zool. Exp.,* **12**: 145–170.

REESE, A. M., 1942. The old starfish-clam question. *Science,* **96**: 513.

SAWANO, E., AND K. MITSUGI, 1932. Toxic action of the stomach extracts of the starfishes on the heart of the oyster. *Sci. Rep. Tohoku Imp. Univ.,* **7**: 79–88.

SCHIEMENZ, P., 1895. Wie offen die Seestern Austern? Mittheilungen des Deutschen Seefishcherievereins Bd. 12 No. 6: 102–118. (Translated into English by Allen, 1896.)

SMITH, J. E., 1937. The structure and function of the tube feet in certain echinoderms. *J. Mar. Biol. Assoc.,* **22**: 345–357.

SMITH, J. E., 1947. The activities of the tube feet of *Asterias rubens* L.; I. The mechanics of movement and posture. *Quart. J. Micr. Sci.,* **88**: 1–14.

TAMURA, T., 1929. The power of the adductor muscle of the oyster, *Ostrea circumpicta. Sci. Rep. Tohoku Imp. Univ.,* **4**: 259–279.